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ANNUAL SURVIVAL RATES OF FEMALE HOODED MERGANSERS AND WOOD DUCKS IN SOUTHEASTERN MISSOURI

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ABSTRACT.—Successful conservation and management, particularly of harvested species, relies on accurate estimates of population demographics. In addition, estimates of survival and longevity allow more accurate modeling of evolutionary life-history trade-offs within and between species. We estimated survival rates for box nesting female Hooded Mergansers (*Lophodytes cucullatus*) and Wood Ducks (*Aix sponsa*) in southeastern Missouri during 1987–1997 and 1987–1993, respectively. Hooded Merganser survival rates varied annually and ranged from 0.42–1.0 ($\bar{x} = 0.66 \pm 0.04$). Wood Duck survival did not vary significantly over time and averaged 0.63 ($\pm$ 0.02). Mean annual survival rates and capture probabilities were similar for the two species ($\chi^2 = 0.49$, df = 1, $P > 0.05$; $\chi^2 = 0.02$, df = 1, $P > 0.05$). Annual variation in Hooded Merganser survival rates was an important component of this species' population ecology, but was not related to winter weather conditions, harvest rates, breeding season rainfall, or nesting parameters. Our female Wood Duck survival rates were higher than survival estimates for other adult females in the north-central subpopulation, but were comparable to some estimates for adult females that breed in southern and mid-Atlantic states. *Received 12 May 1998, accepted 5 Sept. 1998.*

Estimates of annual survival are important for comparative studies of life-history strategies between species (Krementz et al. 1989) and for modeling population demographics for conservation and management. Annual survival rate estimates are available for certain geese (tribe Anserini) and dabbling ducks (tribe Anatini) traditionally important to hunters (Johnson et al. 1992). Except for the Common Eider (*Somateria mollissima*; Krementz et al. 1996), survival estimates based on modern survival estimation procedures are completely lacking for most seaducks (tribe Mergini), despite increased harvest pressure in recent years (U.S. Fish and Wild. Serv., unpubl. data).

Hooded Mergansers (*Lophodytes cucullatus*) are among the least studied of all Mergini (Dugger et al. 1994). Attempts to estimate survival rates are difficult because of their low harvest rate, secretive behavior, year-round occurrence in low densities, and preference for forested wetlands. However, Hooded Mergansers nest in man-made boxes, and capture of these females can provide mark-recapture samples large enough to estimate survival rates (Dugger et al. 1994).

Over much of their range Hooded Mergansers occur sympatrically with Wood Ducks (*Aix sponsa*, tribe Anatini; Livezey 1986) providing an opportunity for comparison of survival estimates. The two species are similar in body size (HM, 540–725 g; WD, 530–680 g; Bellrose and Holm 1994), both nest in tree cavities, and both rely on forested wetlands

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during the breeding season. However, these species differ considerably in many aspects of their biology and might be expected to exhibit differences in annual survival rates. Hooded Mergansers are carnivorous, forage by diving, and exhibit delayed maturation (first breed at ≥2 years old; Dugger et al. 1994). In contrast, Wood Ducks are omnivorous, forage near the water's surface, and most breed as yearlings (Bellrose and Holm 1994). Based on the difference in age at first breeding and phylogeny (Krementz et al. 1997), we predict that Hooded Mergansers experience higher annual survival rates than Wood Ducks (Ricklefs 1973, Wittenberger 1979). In this paper we estimate annual survival rates of box nesting female Hooded Mergansers and Wood Ducks in southeastern Missouri and compare mean annual survival rates of these two species.

TABLE 1. The number of Hooded Merganser nesting attempts and nest success in southeastern Missouri 1987–1997.

Year	Nest attempts[a]	Nest success rate[b] (%)
1987	17	88.2
1988	32	84.4
1989	37	62.2
1990	35	77.1
1991	37	73.0
1992	59	35.6
1993	48	39.6
1994	64	51.5
1995	38	73.7
1996	43	58.1
1997	50	56.0

[a] Total number of nests initiated by Hooded Mergansers in southeast Missouri.

[b] Hooded Merganser nest success (number of successful nests/total number of nest attempts).

STUDY AREA AND METHODS

The study was conducted on the Duck Creek Wildlife Conservation Area (WCA) and Mingo National Wildlife Refuge (NWR) in southeastern Missouri. These adjoining areas comprise Mingo Swamp, the largest contiguous block of bottomland hardwood forest in Missouri (11,174 ha). For a detailed description of the habitat types available in Mingo Swamp see Heitmeyer and coworkers (1989). Approximately 85 boxes were available to nesting females in all years of the study on Mingo NWR, and 100–120 nest boxes were available for nesting birds on Duck Creek WCA during 1987–1993, and most nest boxes were equipped with predator guards to reduce predation by raccoons (*Procyon lotor*). After the nesting season in 1993, approximately 50 boxes were removed on Duck Creek WCA and the Wood Duck nesting study was terminated. Capture of Hooded Mergansers continued on both Mingo NWR and Duck Creek WCA through 1997.

Nest boxes were cleaned, repaired when necessary, and filled with wood chips before each nesting season. Hooded Mergansers and Wood Ducks were captured in nest boxes between 1 February and 15 August each year during 1987–1997 and 1987–93, respectively. We checked boxes at 2–4 week intervals and captured nesting females of both species during the third week of incubation. Unmarked females were banded with U.S. Fish and Wildlife Service leg bands, and band numbers of previously marked birds were recorded. All breeding females of both species captured in nest boxes were used in our analysis, including Wood Ducks that bred as yearlings. Although both Hooded Merganser and Wood Duck ducklings were web-tagged in boxes at hatching, sample sizes of known-age birds were too small to analyze by age class.

We constructed mark-recapture matrices for Hooded Mergansers (11 years) and Wood Ducks (7 years) and used Jolly-Seber mark-recapture models for open populations to estimate survival for both species (Pollock et al. 1990). Program JOLLY computes point estimates, their associated variances, goodness-of-fit tests, and likelihood ratio tests for five open population models (Pollock et al. 1990). We used model goodness-of-fit tests and likelihood ratio tests between models to select the model that provided the best fit for each data set (Pollock et al. 1990). We then compared Wood Duck and Hooded Merganser mean annual survival rates and capture probabilities using the program Contrast (Hines and Sauer 1989) and the methods described by Sauer and Williams (1989). All analyses were performed on an IBM computer under DOS.

Our analysis suggested time dependent variation was an important component of Hooded Merganser survival, so we attempted to identify factors that might be correlated with merganser annual survival rates. We correlated Hooded Merganser survival estimates for each year with annual harvest (USFWS, unpubl. data), winter weather conditions (rainfall, temperature) in the Mississippi Alluvial Valley, and rainfall in Mingo Swamp from March through September. We also correlated Hooded Merganser survival with the number of nesting attempts and nest success on Mingo NWR and Duck Creek WCA (Table 1). These reproductive variables might be expected to index local Hooded Merganser nesting density, and therefore represent the potential for permanent emigration from our study sites.

Although specific wintering areas for birds in our population are largely unknown, the Mississippi Alluvial Valley is the closest region with suitable wintering habitat, and females nesting in Mingo Swamp have been recovered from this region (Dugger et al. 1994). We used mean daily temperature and monthly rainfall totals recorded at two sites in each of three states (Arkansas, Mississippi, and Louisiana) October

TABLE 2. Annual survival estimates and associated capture probabilities for female Hooded Mergansers and Wood Ducks nesting in southeastern Missouri.

	Survival probability (SE)		Capture probability (SE)	
Year	Hooded Merganser	Wood Duck	Hooded Merganser	Wood Duck
1987	0.58 (0.17)	[a]		
1988	0.86 (0.16)	[a]	0.78 (0.19)	0.71 (0.07)
1989	1.00 (0.25)	[a]	0.43 (0.13)	0.77 (0.05)
1990	0.42 (0.11)	[a]	0.37 (0.12)	0.55 (0.05)
1991	0.97 (0.15)	[a]	0.53 (0.12)	0.48 (0.05)
1992	0.54 (0.12)	[a]	0.69 (0.13)	0.51 (0.06)
1993	0.55 (0.12)	[a]	0.59 (0.13)	0.66 (0.08)
1994	0.52 (0.13)		0.71 (0.14)	
1995	0.45 (0.12)		0.65 (0.15)	
1996			0.66 (0.16)	
Mean	0.66 (0.04)	0.63 (0.02)	0.60 (0.05)	0.61 (0.04)

[a] Recapture data from these years were available to estimate constant survival rate for Wood Ducks.

through January for each year (National Climatic Data Center) to index winter habitat conditions. We used total rainfall during March through September collected at Advance, Missouri (National Climatic Data Center) to index local habitat conditions during the breeding and post-breeding season when Hooded Mergansers are present in Mingo Swamp.

RESULTS

We used individual capture histories of 151 Hooded Merganser and 512 Wood Duck females to estimate annual survival. Model A, from Program JOLLY, with time-dependent capture probabilities and survival rates provided the best fit for the Hooded Merganser data ($\chi^2 = 19.61$, df = 12, $P > 0.05$). Model A also fit the Wood Duck data ($\chi^2 = 17.52$, df = 12, $P > 0.05$) as did Model B, a reduced parameter model with constant survival rates and time-dependant capture probability ($\chi^2 = 18.41$, df = 16, $P > 0.05$). The likelihood ratio test between Models A and B ($\chi^2 = 0.90$, df = 4, $P > 0.05$) suggested Model B provided the most parsimonious fit for the Wood Duck data. Jolly-Seber models estimate survival through sample k-2, and capture probability for samples 2 through k-1 (model A) or k (model B). Thus, we had 9 estimates of annual survival and capture probability for Hooded Mergansers (1987–1995) and 6 estimates of capture probability (1988–1992) for Wood Ducks with a single estimate of constant survival (Table 2). Hooded Merganser survival rates ranged from a low of 0.42 in 1990 to a high of 1.0 in 1989 with a mean of 0.66 (± 0.04 SE) with 95% confidence limits of 0.59–0.73 (Table 2). Wood Duck annual survival was 0.63 (± 0.02) with 95% confidence limits of 0.59–0.68 (Table 2). The mean annual survival of Hooded Mergansers was not significantly different than Wood Duck annual survival ($\chi^2 = 0.49$, df = 1, $P > 0.05$).

Capture probability for Hooded Mergansers varied annually from a low of 0.37 in 1990 to a high of 0.78 in 1988 (Table 2). Wood Duck capture rates also exhibited annual variation, ranging from 0.51 in 1992 to 0.77 in 1989 (Table 2). Mean capture probabilities did not differ between species ($\chi^2 = 0.02$, df = 1, $P > 0.05$). In addition, we observed no significant correlation between Hooded Merganser survival rates and annual harvest, winter weather conditions (temperature and rainfall), breeding season rainfall, or Hooded Merganser nesting parameters (all $P > 0.05$).

DISCUSSION

Hooded Merganser and Wood Duck annual survival estimates from our study were generally higher than those reported for other duck species (Johnson et al. 1992). However, because our estimates were for birds using nest boxes with some protection from predatory raccoons, comparisons with other species must be made with caution. Nevertheless, Hooded Mergansers in our study had substantially lower mean annual survival rates than the Common Eider ($\bar{x} = 0.87$; Krementz et al. 1996), the only other member of Mergini for which estimates are available. Yearly survival rates for Hooded Mergansers during 1988,

1989, and 1991 were comparable with those for Common Eiders (Krementz et al. 1996); rates for other years were substantially lower. Wood Duck survival in our study was higher than or comparable to other estimates available for female Wood Ducks (Johnson et al. 1986, Nichols and Johnson 1990, Kelley 1997), including estimates from a South Carolina box-nesting population ($\bar{x}$ = 0.55, Hepp et al. 1987). Wood Duck females are strongly philopatric to nest sites (nearly 100%), so mark-recapture survival estimates that include a measure of capture site fidelity (nest boxes in this case) can be comparable to band recovery estimates (Hepp et al. 1987). Whether our high survival rates reflect general regional differences in survival of eastern Wood Ducks (Nichols and Johnson 1990) or a survival benefit associated with box-nesting remains unclear. Wood Ducks breeding in Missouri are included in the "north-central" sub-population of Bowers and Martin (1975) and Kelley (1997), but exhibit survival rates much higher than band recovery estimates for adult females in this region (Kelley 1997). Our Wood Duck females exhibited survival rates most similar to adult females in the southern population of the Mississippi Flyway ($\bar{x}$ = 0.61; Kelley 1997) and the mid-Atlantic population of the Atlantic Flyway ($\bar{x}$ = 0.63; Kelley 1997).

Mean survival did not differ between Hooded Mergansers and Wood Ducks, although in three of nine years Hooded Merganser survival was higher than the constant rate estimated for Wood Ducks (Table 2). This is inconsistent with life-history theory which predicts that birds with delayed maturation should experience higher annual survival (Wittenberger 1979), but consistent with analyses showing survival rates are correlated with body size and breeding latitude in waterfowl (Arnold 1988). Maybe more important than the comparison of mean survival rates was our observation that annual variation was an important component of Hooded Merganser, but not Wood Duck, survival. Differences in diet, foraging method, and habitat requirements may make Hooded Mergansers more sensitive to local fluctuations in food resources or water conditions during reproduction or winter, with increased mortality or emigration during years when habitat conditions are poor. None of the harvest, breeding season rainfall, density-dependent factors, or winter weather variables we investigated were significantly related to variation in Hooded Merganser survival. However, we did not quantify food availability on the breeding grounds directly and because information on migration patterns and winter site fidelity for Hooded Mergansers is lacking we may not have compared our Hooded Merganser survival rates with the most appropriate winter or breeding season weather conditions. Very little information exists concerning Hooded Merganser foraging ecology or foraging habitat characteristics (Dugger et al. 1994), consequently, determining the climatic factors that index habitat conditions throughout the Hooded Merganser annual cycle will be difficult.

We believe our survival estimates for both species are unbiased, but some behavioral responses such as permanent emigration from the study area cannot be distinguished from "deaths" by Jolly-Seber models and can result in negatively biased survival estimates (Pollock et al. 1990). Wood Ducks are strongly philopatric (Hepp et al. 1987), but data are lacking to estimate philopatry for Hooded Mergansers or to make direct quantitative comparisons with Wood Ducks. We believe that Hooded Mergansers are strongly philopatric to general nesting areas (e.g., Zicus 1990), but not as philopatric as Wood Ducks to specific nesting boxes. Factors that might have caused Hooded Merganser females to have left the study site or chosen not to nest in boxes in subsequent years (low nest success or high breeding density) were not correlated with annual survival as we might expect if permanent emigration were common. Furthermore, in Minnesota, distances moved by Hooded Mergansers between nesting sites each year were not related to nest success (Zicus 1990), suggesting that variation in nest success does not affect philopatry. Habitat conditions in Mingo Swamp could have affected Hooded Merganser use of boxes, but it is unlikely that these effects would be permanent. Finally, we do not believe that nest boxes were limiting for Hooded Mergansers or that competition for nest sites led to higher permanent emigration by Hooded Mergansers from Mingo Swamp. Hooded Merganser populations were substantially lower than Wood Duck populations each year (Dugger 1991)

and the annual number of Hooded Merganser nest attempts remained low in relation to box availability. In addition, Hooded Mergansers initiate nests on average 3–4 weeks earlier than Wood Ducks, thereby reducing the potential for nest site competition between the two species (Dugger et al. 1994).

Overall mean Hooded Merganser survival in this study was lower than a previous estimate (Dugger et al. 1994), and this earlier analysis did not detect any significant annual variation in survival rates. As more data were collected and added to the analysis, estimate precision increased, mean annual survival decreased, and annual variation became an important component of Hooded Merganser survival. The increased variation in annual survival estimates and changes in the long-term mean associated with additional years of study on Hooded Mergansers illustrate the importance of long-term data sets. Continued banding effort and more information concerning Hooded Merganser habitat use, foraging ecology, and age-specific survival rates are needed to understand the factors affecting annual variation in survival of this species.

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